



Seed germination and predation of the tropical monocarpic palm tree *Corypha umbraculifera*

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ABSTRACT: *Corypha umbraculifera* L., the long lived monocarpic palm belonging to Arecaceae, is rare in the wild and is a possible candidate, which can be developed as an economic plant in Asia. However, little information is available about propagation of this species from seeds. Thus, we aimed to investigate the basic seed biology of this species and to facilitate its propagation and conservation. Effects of light and temperature on seed germination were studied. Morphology of seed germination and embryo: seed ratio were recorded. Seed predation percentages, initial moisture content and nutrient content were determined and optimum storage conditions identified. The highest germination percentage was in light/dark at 25 °C. In two trials, of 38.66 and 31.66 % of the seeds were predated. Total energy value of seeds was higher than that of *Cocos nucifera*, a common known polycarpic palm. Seeds of *C. umbraculifera* have morphophysiological dormancy as evidence by embryo growth prior to radicle emergence and the relatively long time (42–49 days) taken for completion of germination. Low predation percentage and slow germination rate indicate that the predator satiation hypothesis is not sufficient to describe the evolution and existence of monocarpy in *C. umbraculifera*. Decreased viability during dry storage at ambient room conditions and a moisture content of 16 ± 3 % indicate that seeds have intermediate storage behaviour. Storage in open polythene bags at 8 °C is suggested as the best storage condition for *C. umbraculifera* seeds.

KEY WORDS: Conservation, *Corypha umbraculifera*, Morphophysiological dormancy, Seed predation, Seed storage, Semelparity.

INTRODUCTION

The talipot palm (*Corypha umbraculifera* L., Arecaceae) is a long-lived monocarpic tree with an extended period of vegetative growth of 30–80 years. The species is found growing along the Malabar Coast of south western India and in Sri Lanka (Johnson, 1998; Dassanayake, 2000). The distribution of the talipot palm is associated with human habitats (Dassanayake, 2000), and it is considered to be rare in the wild (Gadgil and Chandran, 1988; Johnson, 1998). In fact, although *C. umbraculifera* exhibits natural distribution, it is not found in the wild (Dassanayake, 2000). Leaves of the talipot palm have been used for the documentation of Thripitaka (Buddhist scriptures) (Johnson, 1998). It is speculated that this palm was introduced to Sri Lanka for the documentation of ancient Buddhist texts (Dassanayake, 2000). Over exploitation of this species in Thailand and India (Gadgil and Chandran, 1988; Johnson, 1998) has made the talipot palm rare. *C. umbraculifera* has been categorized as a data deficient species in the Red List of Threatened Species, IUCN (1998), while in the list of threatened and rare ornamental plants prepared by Khoshbakht and Hammer (2007) it is listed as a rare ornamental species.

Johnson (1998) has reported that *C. umbraculifera* is a promising palm with agroforestry potential and thus a

possible candidate for development as an economic plant in Asia. *C. umbraculifera* is a multipurpose palm that yields a fine combination of commercial and subsistence products (Johnson, 1998; Khoshbakht and Hammer, 2007). The major products produced by the talipot palm are its sap and starch from its stem (Johnson, 1998; Khoshbakht and Hammer, 2007). One-hundred to 250 kg of edible starch can be extracted from the stem of a mature tree before its fruiting (Dassanayake, 2000). A tree yields two liters of sap per day for 3–4 months, which is used to produce sugar, wine, alcohol and vinegar (Johnson, 1998). Minor products include the use of the hard seeds to manufacture buttons and beads (Johnson, 1998; Dassanayake, 2000; Khoshbakht and Hammer, 2007). Leaves are used to produce writing material, baskets, and mats (Dassanayake, 2000; Khoshbakht and Hammer, 2007). In addition, leaves also are used to feed livestock and for thatching (Johnson, 1998). These facts demonstrate that the talipot palm is an ideal species for management and domestication (Johnson, 1998). Thus, conservation of this palm is of extreme importance, but to do this we need to be able to propagate the species from seeds and to store seeds in germplasm banks.

Basic information on seed biology is essential for the conservation of rare species as many species depend on seeds for propagation (Baskin and Baskin, 1998). To



produce the maximum number of healthy seedlings from the minimum number of seeds, we need to determine the dormancy breaking and germination requirements as well as appropriate long-term storage methods to maintain viability of seeds to be used for propagation in the future (Baskin and Baskin, 1998). To our knowledge, only a few studies have been conducted on the seed biology of *C. umbraculifera*. Viji *et al.* (2013) found that *C. umbraculifera* seeds have a very low germination percentage. According to the latter research conducted by Viji *et al.* (2015), talipot palm seeds require 64–77 days to complete germination. Further, they reported that this palm has the remote type seed germination, i.e. the shoot develops inside the cotyledonary sheath and emerges through a cleft formed in it. Although Viji *et al.* (2015) described the morpho-anatomical changes during the germination, they have neither described the germination requirements nor the dormancy class of the seeds. However, Baskin and Baskin (2014) speculated that seeds of *C. umbraculifera* have morphological observations recorded by Koebernik (1971) and by Esenowo and Adebona (1990). However, morphophysiological dormancy has not been proven for *C. umbraculifera*. Only limited information is available on seed germination of other *Corypha* species. Khondker *et al.* (2010) reported that seeds of *C. talliera* require about 48 days to complete germination, while Naiola and Nurhidayaf (2009) reported that *C. utan* seeds are dormant.

Seed storage behavior is a very important component of the seed biology of a species. Knowledge of seed storage behavior is important in handling and storing seeds. Viji *et al.*, (2015) reported that after 35 days of drying, 50 % of the *C. umbraculifera* seeds became non-viable, and, thus, they categorized the seeds as being recalcitrant. They further stated that its seeds have > 30 % seed moisture content at the dispersal maturity. Many palm species produce seeds with nonorthodox (intermediate to recalcitrant) storage behaviour, whereas only some have seeds that are orthodox (Dickie *et al.*, 1992). It is very difficult to store nonorthodox seeds since they are sensitive to desiccation. In addition nonorthodox palm seeds are often sensitive to low temperature (Hong and Ellis, 1994), making it very difficult to store seeds of palm species. Moist storage, partial desiccation (Chin, 1994) and anesthetic storage (Sowa and Roos, 1991) are some of the methods used to store nonorthodox seeds. However, moist storage is the least expensive method, since the other two methods require sophisticated equipment. In the moist storage method, precautions are taken to reduce water loss from the seeds, and temperature and O₂ concentration are kept at minimum to reduce the deterioration and pathogenic attacks (King and Robberts, 1980). Moistened saw dust, charcoal,

peat, sand or coir dust have been used as the storage medium to reduce the water loss. However, none of the moist storage methods have been tried for the storage of *C. umbraculifera* seeds.

The reason why plants die after a single reproduction event in monocarpic species is favored by natural selection has inspired many theories in evolutionary biology (Janzen, 1976; Schaffer and Rosenzweig, 1977; Gadgil and Prasad, 1984; Young, 1990). Most of the theoretical approaches to the evolution of the monocarpic strategy assume a tradeoff between present and future reproduction events (Young and Augspurger, 1991). According to the hypothesis proposed by Janzen (1976), monocarpic strategy and mast fruiting strategy are adaptations for high predator pressure. This model proposes that natural selection for predator satiation favors the evolution of monocarps (Janzen, 1976). When a monocarp dies after fruiting, herbivores that depend on it are depleted of their food source (Janzen, 1976). The abundant supply of seeds ends with the death of the plant. Strong reproductive synchrony is a common phenomenon among monocarps. For monocarps that synchronize reproduction, the gap between two mast fruiting events is usually longer than a year (Janzen, 1976). Therefore, seed predators cannot depend on monocarps exclusively. Seed predators of monocarps are usually extreme generalists (Janzen, 1976).

Thus, the main objectives of current research were to gather the basic seed biology information for propagation of this rare palm species and to use this species to test the predator satiation hypothesis. To achieve these objectives, seed germination, seed nutrient content, seed predation and seed storage of the *C. umbraculifera* were studied.

METHOD AND MATERIAL

Study Species

Corypha umbraculifera L. is a fan palm and is one of the largest palms in the world, attaining heights of 20–25 m. The inflorescence of *C. umbraculifera* is the largest one borne on any plant (Tomlinson, 2006) and contains approximately 23.9 million florets (Fisher *et al.*, 1987). Fruits are globose, grayish green and 3–4 cm in diameter. Each fruit contains a single seed. Seeds are narrowly grooved and have a diameter of about 2 cm.

Seed collection and general laboratory procedures

Ripened fruits were collected from the ground near four *C. umbraculifera* trees growing in the palm garden of the Royal Botanical Gardens, Peradeniya in Sri Lanka. Fruit collection was conducted from February to April 2015, during the fruiting period of these four *Corypha* trees. Fruits were placed in polythene bags and taken to the University of Peradeniya, Peradeniya, Sri Lanka. Pulp of the fruits was removed and “seeds”



were extracted. Extracted “seeds” were air dried for 24 hours. Extracted “seed” consisted of the true seed encapsulated by the endocarp. Hereafter, this structure will be referred to as the seed. Experiments were initiated within 1 week of collection. The ambient temperature of the laboratory was ~ 27 °C, whereas the relative humidity was ~ 80 %. Seeds were selected randomly for each experiment.

Experiments to determine seed dormancy

Standard germination test

The objective of this experiment was to determine whether seeds are dormant or not. Four samples containing four replicates of eight seeds were incubated on three layers of moistened tissues papers in plastic trays at 25 and at 15 °C in light/dark (14/10 hr) or in complete darkness (25 °C is the annual average temperature of the Peradeniya area and 15 °C is the average minimum temperature during December to February). These experiments were conducted in seed incubators with artificial white fluorescent light. Complete darkness was provided by covering the trays with aluminum foil. Seed samples were observed at seven-day intervals for germination. Seeds in complete darkness were observed in 14-day intervals under very low light conditions. The definition for germination was the emergence of the cotyledonary petiole. The number of days from sowing to the emergence of the cotyledonary petiole was recorded.

Morphological changes during germination

The objective of this part of the study was to record germination morphology of this species and determine the germination type. Sixty seeds were incubated on three layers of moistened tissue papers in plastic trays at ambient laboratory temperature (~ 27 °C) and light (artificial florescent light and natural light penetrated through windows during the day and complete darkness at night) conditions. A sample of five seeds was selected randomly in each week for 12 weeks. Seeds were observed for external morphological changes and photographs were taken with a Sony Cyber-shot DSC-W30 digital camera.

Change of embryo length: seed length (E:S) ratio

The objective of this experiment was to determine if *C. umbraculifera* embryos grow within the seed prior to seed germination. If the embryo grows within the seed prior to germination, the seed is categorized as having an underdeveloped embryo. Sixty seeds were incubated on three layers of moistened tissue papers in plastic trays at ambient laboratory temperature and light conditions. A sample of five seeds was selected randomly in each week for 12 weeks. Seeds were dissected along their vertical axes. Haustorium (E), cotyledonary petiole, radicle, shoot and seed (S) lengths (as shown in Fig. 1) were measured to the nearest 1 mm using a ruler. Haustorium length: seed length ratio (E: S ratio) was calculated for

each stage. This measurement was taken as the E:S ratio because haustorial part of the embryo is the only part of the embryo that develops inside the seed. A digital camera was used to photograph the embryos at different stages of development.

Effect of light on shoot emergence

This study was conducted to determine the effect of light on shoot emergence. After the emergence of the cotyledonary petiole, eight seeds were incubated on three layers of moistened tissue paper in glass jars at 25 °C in light/dark or in complete darkness as explained above. Seeds were observed at one-week intervals to check for radicle and shoot emergence. Radicle and shoot emergence of individual seeds were monitored. Number of days from protrusion of the cotyledonary petiole to radicle and shoot emergence was determined.

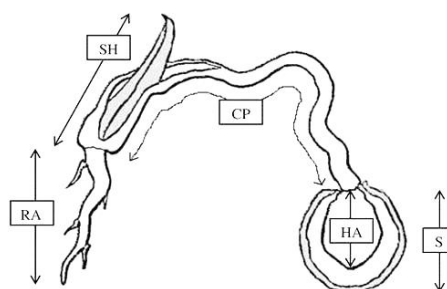


Fig. 1. Different measurements taken from the germinating *C. umbraculifera* seed. S, seed length; HA, haustorium length; CP, length of the cotyledonary petiole; SH, shoot length; RA, radicle length.

Seed predation frequency

This experiment was conducted to determine the amount of seed predatory pressure on *C. umbraculifera* seeds. Six replicates of 25 seeds were placed on ground in six different locations within a diameter of 50 m from the fruiting *C. umbraculifera* trees. Seed samples were observed at 3-day intervals for 30 days. Number of removed seeds and remaining seeds was determined. This experiment was conducted two times during February and April.

Estimation of the nutrient content of seeds

The purpose of these experiments was to determine the nutrient content of seeds to better understand the significance of the seeds as a food source for seed predators. Total lipid, carbohydrate and protein contents of the endosperm of the seeds were determined using the standard protocols by Bligh and Dyer (1959), Snell and Snell (1970) and Layne (1957), respectively. Ten randomly selected seeds were used for the nutrient analysis. Crushed seed powder of the 10 seeds was mixed thoroughly, and five random samples were taken for each analysis.

As recommended by United States Food and Drug



administration, energy value of seeds was calculated using the theoretical calculations of Stewart (1992). These energy values were compared to those reported in literature for *Cocos nucifera*, a common polycarpic palm.

Seed Storage of *Corypha umbraculifera*

The purpose of these experiment was to determine a suitable storage procedure for *C. umbraculifera* seeds. These experiments will further be used to determine the storage behaviour of the *C. umbraculifera* seeds.

Seed moisture content

The objective of this study was to determine the seeds storage behaviour of *C. umbraculifera* seeds using the moisture content (MC) at dispersal. Orthodox seeds have an initial seed MC of 10–30 % at dispersal, whereas recalcitrant seeds have 20–45 % MC at dispersal. An analytical balance was used to weigh ten seeds individually to the nearest 0.0001 g, which were then oven-dried at 120 °C for 3 hours (ISTA, 2012). Each seed was reweighed after oven drying. Dry mass and fresh mass of seeds were used to determine the MC (dry mass basis [%]).

Effect of different storage treatments on seed viability

This experiment was conducted to determine the optimum storage conditions for *C. umbraculifera* seeds. Seeds were stored according to the following moist storage methods. In each experiment, sealed polythene bags and moist coir dust were used to reduce the moisture loss. Open polythene bags were used as controls. Three replicates of eight seeds were used for each storage experiment. After the storage period, seed samples were incubated on three layers of moistened tissue paper in plastic trays at 25 °C in light/dark conditions. Seeds were observed at one-week intervals for 8 weeks. Germination percentage was recorded for each replicate. Emergence of the cotyledonary petiole was the criterion for germination. The remaining seeds were dissected to check the embryo viability, i.e. white firm (viable) embryo vs. gray soft (nonviable) embryo.

- Stored at 25 °C for one month in sealed polythene bags containing moist coir dust
- Stored at 8 °C for one and three months in sealed polythene bags
- Stored at 25 °C for one and three months in open polythene bags
- Stored at 8 °C for one and three month in open polythene bags

Analysis of data

Germination data and viability data were analyzed with the binary logistic regression procedure (Schimpf *et al.*, 1977; Brown and Mayer, 1988a, b; Torres and Frutos, 1990; Zhao *et al.*, 2001) in MINITAB statistical software. Number of days taken to radicle or shoot emergence, E: S ratio and growth parameters data were analyzed with one-way ANOVA procedure. Tukey's mean separation procedure was used to determine the

differences between treatments. Graphs were prepared with SIGMA-PLOT and EXCEL softwares.

RESULTS

Experiments to determine seed dormancy

Standard germination test

Seeds incubated in light/dark at 25 °C exhibited the highest emergence of the cotyledonary petiole (96.9 %, Fig. 2). Less than 10% of the seeds germinated at 15 °C in both dark and light/dark conditions within the study period (6 weeks). Compared to seeds incubated at 15 °C, seeds tested at 25 °C had significantly higher germination percentage ($Z = 4.62$, $P < 0.001$). Further, the germination percentage of seeds incubated at 25 °C in light/dark was significantly higher than that of those tested in complete darkness at 25 °C ($Z = 3.71$, $P < 0.001$).

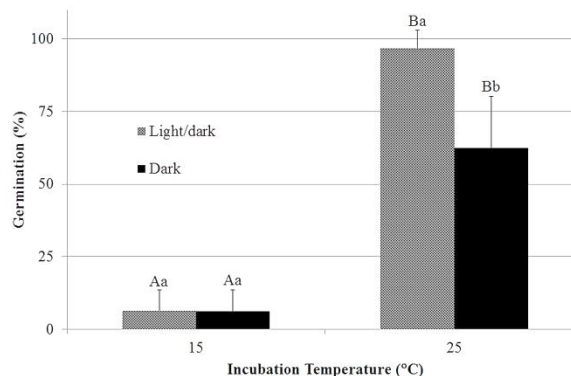


Fig. 2. Cumulative germination of *C. umbraculifera* (emergence of the cotyledonary petiole) seeds incubated in light/dark and dark at 15 and 25 °C for 6 weeks. Different upper case letters indicate significant differences between temperatures within the same light conditions. Different lowercase letters indicate significant differences between light conditions within the same temperature. Bars are \pm SE.

Morphological changes during germination

A mature *C. umbraculifera* seed has a conspicuous endosperm with a small top shaped embryo that differentiated into two regions: the cotyledonary petiole and the cotyledonary blade (Fig. 3A). The cotyledonary petiole was adjacent to the operculum, which a small region of the seed coat that is relatively thin (Fig. 3B). Endosperm of the seed was homogeneous, dry and contained a cavity (Fig. 3A). Germination was marked by the protrusion of the cotyledonary petiole, which ruptured the operculum after about 14 d from the incubation in light/dark at 25 °C (Fig. 3B). As in all the other palms, *C. umbraculifera* exhibited hypogeous type of germination, i.e. the cotyledonary blade did not emerge from the seed coat or above the ground level (Figs. 3C and 3D). The cotyledonary blade developed into a haustorium by the time cotyledonary petiole protruded from the seed coat (Fig. 3D). The haustorium

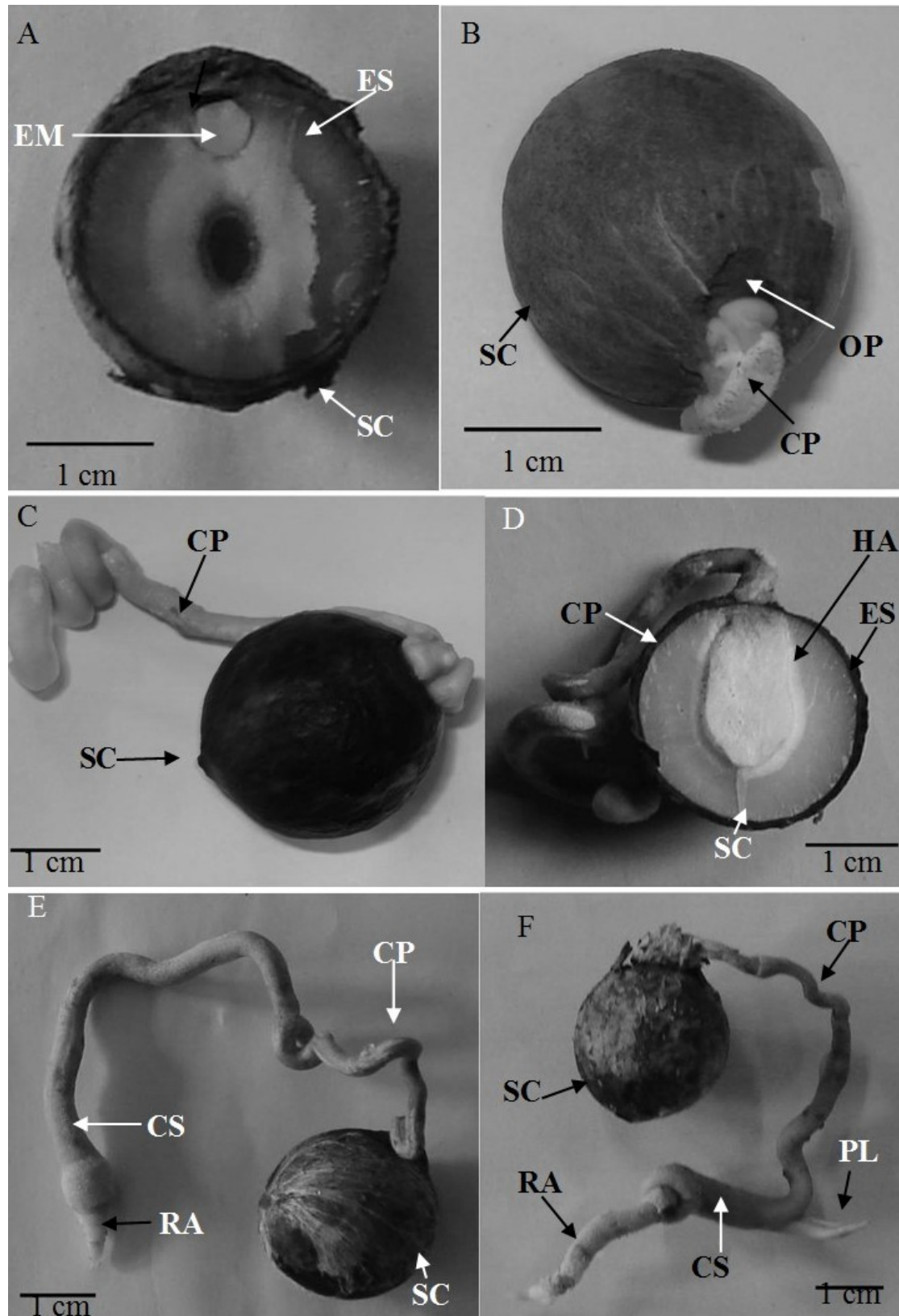


Fig. 3. Different stages of germination of *Corypha umbraculifera* seeds; at dispersed maturity (A), two weeks after sowing (B), five weeks after sowing (C, D), eight weeks after sowing (E) and nine weeks after sowing. CP, cotyledonary petiole; CS, cotyledonary sheath; EM, embryo; ES, endosperm; HA, haustorium; OP, operculum; RA, radicle; SC, seed coat; SH, Shoot.



continued to grow until it filled the whole space of the seed at about 42 d. Since, the germination type of *C. umbraculifera* is remote, the elongation of the cotyledonary petiole moved the seedling ~199.4 mm away from the seed (Fig. 3C). Positive geotropic (downward) development of the cotyledonary petiole pushed the embryonic axis into the soil at about 24 d (Fig. 3E). The seedling developed from the enlarged basal sheath of the cotyledonary petiole. At the time of radicle emergence, the length of the cotyledonary petiole was ~823 % of that of the seed. The radicle (primary root) protruded downward through the base of the cotyledonary sheath at about 42 d (Fig. 3E). The shoot emerged from a split in the cotyledonary sheath at about 42-49 d (Fig. 3F), at which time the length of the shoot was ~135 % of that of the seed. The primary root was replaced by adventitious roots after completion of germination at about 56 d. Thus, the type of germination of *C. umbraculifera* seeds is remote tubular.

Change of embryo length: seed length (E: S) ratio

Initial E: S ratio of the *C. umbraculifera* seeds was 0.14 ± 0.03 (mean \pm SE, Fig. 4). E: S ratio increased to 0.17 ± 0.04 by the time of cotyledonary petiole emergence. The major contributor to the embryo development was the development of the haustorium. The haustorium had elongated ~21 % within the seed by the time of the cotyledonary petiole emergence. The haustorium length: seed length ratio was 0.75 ± 0.06 at the protrusion of the radicle and at the protrusion of the shoot. Thus, the haustorium had elongated ~535 % within the seed prior to radicle and shoot emergence. Haustorium length: seed length ratio at the time of the cotyledonary petiole emergence was not significantly different to that at the time of sowing. However, haustorium length: seed length ratio at radicle emergence was significantly different from that of the mature seed ($F = 287.02$, $P < 0.001$).

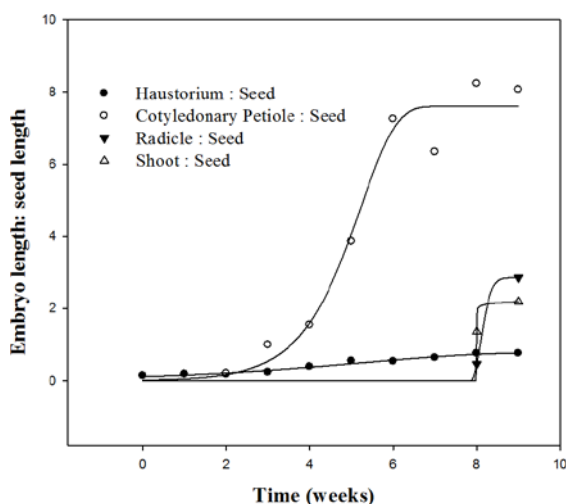


Fig. 4. Embryo length: seed length ratio of *Corypha umbraculifera* seeds during incubation at 25 °C in light/dark. Fitted curves were plotted to see the patterns of embryo development.

Effect of light on shoot emergence

Radicles or shoots did not emerge in germinated (cotyledonary petiole emerged) seeds incubated in darkness despite the light condition (light or dark) under which germination had occurred. If the cotyledonary petiole emerged in the dark, and seeds were then incubated in light, radicles and shoots emerged 6.7 ± 0.9 (Mean \pm SE) and 7.1 ± 0.6 weeks after the emergence of the cotyledonary petiole, respectively. If the cotyledonary petiole emerged in the light and seeds were then incubated in light, radicles and shoots emerged 6.8 ± 0.1 and 9.5 ± 1.7 weeks after the emergence of the cotyledonary petiole, respectively. Time taken for radicle emergence in light, of cotyledonary petiole emerged seeds in light was not significantly different from that of cotyledonary petiole emerged seeds in dark ($t = -0.37$, $P = 0.72$). However, shoots emerged in cotyledonary emerged seeds in dark within a significantly short period of time compared to cotyledonary emerged seeds in light ($t = -5.97$, $p < 0.001$).

Seed predation frequency

Both predation trials showed similar linear patterns. Within the first week, only < 10 % of the seeds had been removed from the locations in both trials. The total observed seed removal was 38.66 and 31.66 % for the first and second trials, respectively during the study period (Fig. 5).

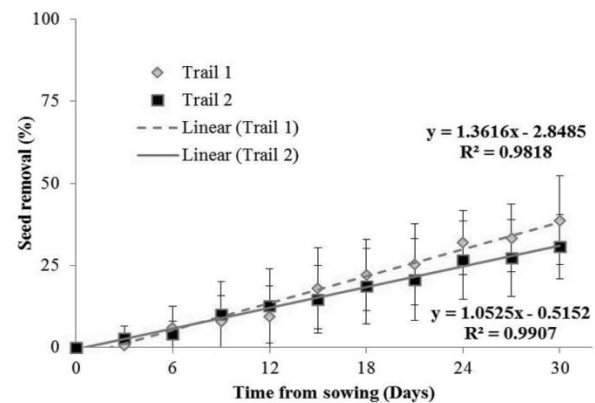


Fig. 5. Percentage of *Corypha umbraculifera* seed removal by predators during 30 days. Error bars are \pm SE. Linear curves were fitted to see the trend of seed removal.

Estimation of the nutrient content of seeds

The average protein concentration of *C. umbraculifera* seeds was 0.47 ± 0.02 % (Mean \pm SE). This amount of protein can provide 1.88 calories per gram of endosperm. The average carbohydrate content of powdered seeds was 10.96 ± 1.8 %. The corresponding energy value was 0.44 calories per gram of endosperm. The average lipid content of three 2 g replicates of powdered seeds was 76.17 ± 2.0 %. This value is equal to 6.85 calories per gram of endosperm. The total energy value of *C. umbraculifera* seeds was 9.17 calories per gram.



Seed Storage of *Corypha umbraculifera*

Seed moisture content

The average fresh mass of *C. umbraculifera* seeds was 9.4 ± 1.6 g (Mean \pm SE), while the dry mass was 7.8 ± 0.9 g. Thus, the moisture content of the seeds at dispersal maturity was 16.0 ± 3.0 % (wet mass basis).

Effect of different storage treatments on seed viability

The cotyledonary petiole emerged from about 88 % of the *C. umbraculifera* seeds while they were stored in sealed polythene bags containing moist coir dust at 25 °C for one month. However, cotyledonary petiole did not emerge from any of the seeds in other storage treatments during the storage period. The highest cotyledonary petiole emergence (75 %) after the storage (during incubation) was for seeds stored sealed bags in moist coir dust at 8 °C (Fig. 6A) and open polythene bags at 25 °C for one month (Fig. 6B). The lowest cotyledonary petiole emergence (25.0 ± 1.0 %) after the storage (during incubation) was recorded in seeds stored in open polythene bags at 8 °C for one month.

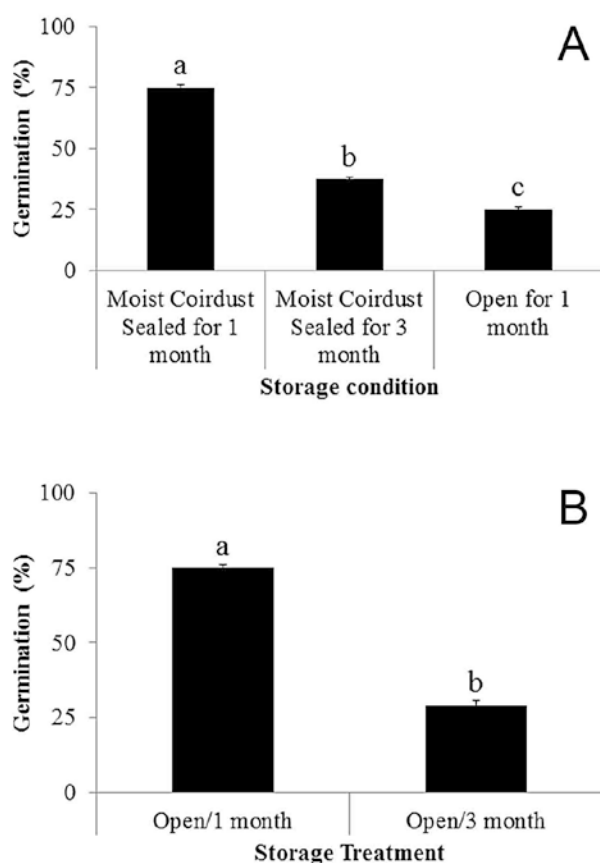


Fig. 6. Germination of *C. umbraculifera* seeds following different storage treatments at A) 8 °C and at B) 25 °C in 1) sealed polythene bags containing moist coir dust for one month and for three months; and 2) open polythene bags for one month and three months. Error bars are \pm SE. Different upper case letters depicts significant statistical differences between storage treatments.

DISCUSSION

A high percentage (96.9 %) of fresh *C. umbraculifera* seeds readily imbibed (visual observation) and germinated in light/dark at 25 °C without any treatment. Thus, it can be concluded that *C. umbraculifera* seeds do not have physical dormancy (PY) or combinational dormancy (PY + PD) (see Baskin and Baskin, 2014 for more information on dormancy classes). In contrast to the high germination percentage found in this study, Viji *et al.* (2013, 2015) stated that the germination percentage of *C. umbraculifera* seeds is very low. The differences between our results and those reported by Viji *et al.* (2013, 2015) may be due to varietal differences or maternal effect. The germination percentage of seeds tested in light/dark was significantly higher than that of seeds incubated in complete darkness ($Z = 3.71$, $P < 0.001$, Fig. 4.1). Thus, germination of *C. umbraculifera* seeds is enhanced by light. Further, the germination percentage of seeds incubated at 25 °C was significantly higher than that at 15 °C ($Z = 4.62$, $P < 0.001$, Fig. 2) suggesting that *C. umbraculifera* seeds like those of most tropical species require high temperatures for germination.

The definition of germination we used in our research was the protrusion of the cotyledonary petiole since it emerges from the seed prior to radicle emergence during the germination process of most palm species (Baskin and Baskin, 1998). Germination (i.e., cotyledonary petiole emergence) of *C. umbraculifera* seeds occurred within ~ 14 days from the initiation of incubation (Fig. 4). However, radicle and shoot emergence, which completed the germination process, required 42-49 days of incubation. Sautu *et al.*, (2007) proposed a 30-day cut-off period to separate dormant and non-dormant seeds, with those that germinate within 30 days being categorized as nondormant. Thus, according to this criterion, seeds of *C. umbraculifera* can be considered as dormant since they required 42-49 days to complete germination. According to the predator satiation hypothesis on monocarpic plants proposed by Janzen (1976), only fast germinating seeds can successfully escape from the satiated predators. Thus, *C. umbraculifera* seeds, germinating at a moderate rate, may not be capable of escaping satiated predators.

Embryo of *C. umbraculifera* elongated ~ 21 % within the seed before the emergence of the cotyledonary petiole. The embryo development percentage was ~ 535 % by the time the radicle emergence. However, development of the cotyledonary blade (with a haustorial function, Viji *et al.*, 2015) exhibited a significant contribution towards embryo development similar to seeds of many other palm species (Baskin and Baskin, 2014). Thus, it can be



concluded that *C. umbraculifera* seeds have underdeveloped embryos that develop within the seed after dispersal. Thus, according to the Baskin and Baskin (2004) seed dormancy classification system it can be concluded that *C. umbraculifera* seeds have a morphological component to their dormancy. Our observations and conclusions are in accordance with those of Baskin and Baskin (2014), who concluded that the embryos exhibit a special type of underdevelopment and that palm seeds have either morphological or morphophysiological dormancy. In palms, the cotyledonary petiole emerges from the aperture created by the displacement of the operculum, and the differentiated embryo (cotyledonary petiole) develops outside the seed before the occurring of radicle and shoot emergence (Baskin and Baskin, 2014). Thus protrusion of the cotyledonary petiole is considered as the criterion for germination of palm seeds. Furthermore, Baskin and Baskin (2007) reported that the E: S ratio of underdeveloped embryos is < 0.5 . The E: S ratio of *C. umbraculifera* seeds was 0.14 ± 0.03 . Thus, the E:S ratio of the *C. umbraculifera* lies within the E: S ratio range of seeds with underdeveloped embryos. These facts confirmed that seeds of *C. umbraculifera* have underdeveloped embryos and that they have a morphological component of dormancy. According to Baskin and Baskin (1998), seeds with morphological dormancy (MD) complete germination within < 30 days. However, seeds with morphophysiological dormancy (MPD) require > 30 days to complete germination. Since *C. umbraculifera* seeds required 42-49 days to complete germination, it can be concluded that they have MPD. Our observations confirm the speculated MPD in *C. umbraculifera* seeds by Baskin and Baskin (2014).

The total *C. umbraculifera* seed removal by predators was 38.66 and 31.66 % during two trials conducted in our research (Fig. 5). These values indicate that there was a significant level of seed predation on *C. umbraculifera* seeds. However, this value might be an over estimation for the actual predation as it indicates only the removal of seeds from the sites. Some of the removed seeds could remain viable if the damage done to them by the predator is insignificant. The dispersal unit of *C. umbraculifera* is the whole fruit consisting of a hard endocarp. This hard endocarp may prevent seeds from being destroyed. Thus, further studies on the behaviour of seed predators and predation studies under different environmental conditions are essential to estimate the predation level on *C. umbraculifera* seeds. Nutritional value of seeds is an important factor that determines the level of seed predation. The total energy of *C. umbraculifera* seeds was determined using the assigning average energy values for proteins, lipids and carbohydrates (Stewart, 1992), and it was calculated to be 9.17 calories per

gram. When the energy level of *C. umbraculifera* seeds was compared to that of *Cocos nucifera* seeds, a polycarpic palm (3.54 calories per gram), (USDA, 2008), we discovered that the total energy content of *C. umbraculifera* was about 2½ folds higher than that of *C. nucifera*. Thus, it can be concluded that *C. umbraculifera* seeds have a high nutrient content. According to the predator satiation hypothesis, monocarps produce seeds with high nutritional value. Having a high nutritive value is important to satiate predators because it enables predators to fulfill their energy requirement by consuming just a few seeds. Thus, the remaining seeds would have a greater opportunity to escape predation (Janzen, 1976). *C. umbraculifera* seeds contained a high fat content (~ 76 % of the dry mass) similar to seeds of many other palms. Fats are considered as one of the most efficient means for storing energy. This observation is in accordance with the predictions of the predator satiation hypothesis (Janzen 1976; Aston *et al.*, 1988). However, the predation rate and the germination behavior of *C. umbraculifera* are not in accordance with the predictions of this hypothesis. High level of predation favors monocarpic behavior in a predictable environment. If the predation stress is low, monocarpy would not be advantageous over polycarpic strategy, because species that exhibit the monocarpic strategy would take several other risks, for example, total reproductive losses in harsh environmental conditions, or death of individual plant prior to reproduction. The low levels of seed predation on a seeds with high nutritive value found in this study is hard to explain. One factor that might have caused the low predation was that this experiment was conducted in a botanical garden where the natural setting is altered. Another factor could be the presence of hard endocarp of the *C. umbraculifera* seeds. Many rodent species detect seeds through olfactory cues (Paulsen *et al.*, 2013). Many seeds release volatile compounds when they are in the imbibed stage and can be sensed by the rodent seed predators (Vander Wall, 1998). Hard endocarp of the *C. umbraculifera* seeds may reduce the release of volatile compounds and thus reduce the seed predation.

The moisture content of *C. umbraculifera* seeds (16 ± 3.0) falls within the MC of seeds with intermediate storage behavior as well as within the MC range of orthodox seeds (Roberts, 1973; Ellis *et al.*, 1990; Berjak and Pammenter, 1997). Decrease in germination percentage (viability) of seeds following open storage suggested that they exhibit intermediate storage behavior. This finding is in accordance with the findings of Viji *et al.* (2013). They suggested that the storage behavior of *C. umbraculifera* seeds is nonorthodox. Since the storage behavior of *C. umbraculifera* seeds is nonorthodox, it is important to take precautions to maintain the viability of seeds



during storage. Based on the results of seed storage experiments, we suggest that the optimal storability of this species could be attained by storing seeds in sealed polythene at 8 °C. *Corypha umbraculifera* is a rare ornamental palm that yields a good combination of economic and subsistence products. It has agroforestry potential and is a strong candidate for being developed as an economic species in Asia. An extensive knowledge on the germination morphology, seed storage behaviour and life history of *C. umbraculifera* is essential for the sustainable development of this species. Therefore, the information generated in this study provides considerable value for conservation purpose and in economic propagation of this species.

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